MOLECULAR BIOLOGY OF THIRD EDITION

Bruce Alberts • Dennis Bray Julian Lewis • Martin Raff • Keith Roberts James D. Watson



BEST AVAILABLE COPY

GARLAND STAFF

Text Editor: Miranda Robertson Managing Editor: Ruth Adams

Illustrator: Nigel Orme

Molecular Model Drawings: Kate Hesketh-Moore Director of Electronic Publishing: John M-Roblin

Computer Specialist: Chuck Bartelt Disk Preparation: Carol Winter Copy Editor: Shirley M. Cobert Production Editor: Douglas Goertzen Production Coordinator: Perry Bessas

Indexer: Maija Hinkle

Bruce Alberts received his Ph.D. from Harvard University and is currently President of the National Academy of Sciences and Professor of Biochemistry and Biophysics at the University of California, San Francisco. Dennis Bray received his Ph.D. from the Massachusetts Institute of Technology and is currently a Medical Research Council Fellow in the Department of Zoology, University of Cambridge. Julian Lewis received his D.Phil. from the University of Oxford and is currently a Senior Scientist in the Imperial Cancer Research Fund Developmental Biology Unit, University of Oxford. Martin Raff received his M.D. from McGill University and is currently a Professor in the MRC Laboratory for Molecular Cell Biology and the Biology Department, University College London. Keith Roberts received his Ph.D. from the University of Cambridge and is currently Head of the Department of Cell Biology, the John Innes Institute, Norwich. James D. Watson received his Ph.D. from Indiana University and is currently Director of the Cold Spring Harbor Laboratory. He is the author of Molecular Biology of the Gene and, with Francis Crick and Maurice Wilkins, won the Nobel Prize in Medicine and Physiology in 1962.

© 1983, 1989, 1994 by Bruce Alberts, Dennis Bray, Julian Lewis, Martin Raff, Keith Roberts, and James D. Watson.

All rights reserved. No part of this book covered by the copyright hereon may be reproduced or used in any form or by any means-graphic, electronic, or mechanical, including photocopying, recording, taping, or information storage and retrieval systems—without permission of the publisher.

Library of Congress Cataloging-in-Publication Data

Molecular biology of the cell / Bruce Alberts . . . [et al.].—3rd ed.

p. cm.

Includes bibliographical references and index. ISBN 0-8153-1619-4 (hard cover).---ISBN 0-8153-1620-8 (pbk.) 1. Cytology. 2. Molecular biology. I. Alberts, Bruce.

[DNLM: 1. Cells. 2. Molecular Biology. QH 581.2 M718 1994]

QH581.2.M64 1994 574.87-dc20

DNLM/DLC for Library of Congress

93-45907

CIP

Published by Garland Publishing, Inc. 717 Fifth Avenue, New York, NY 10022

Printed in the United States of America

15 14 13 12 10 9 8 7 6 5 4 3 2

Front cover: The photograph shows a rat nerve cell in culture. It is labeled (yellow) with a fluorescent antibody that stains its cell body and dendritic processes. Nerve terminals (green) from other neurons (not visible), which have made synapses on the cell, are labeled with a different antibody. (Courtesy of Olaf Mundigl and Pietro de Camilli.)

Dedication page: Gavin Borden, late president of Garland Publishing, weathered in during his mid-1980s climb near Mount McKinley with MBoC author Bruce Alberts and famous mountaineer guide Mugs Stump (1940-1992).

Back cover: The authors, in alphabetical order, crossing Abbey Road in London on their way to lunch. Much of this third edition was written in a house just around the corner. (Photograph by Richard Olivier.)

alcohol

Polar organic molecule that contains a functional hydroxyl group (—OH) bound to a carbon atom that is not in an aromatic ring.

An example is ethyl alcohol.

aldehyde

Organic compound that contains the —CH=O group. An example is glyceraldehyde. Can be oxidized to an acid or reduced to an alcohol.

alga (plural algae)

Informal term used to describe a wide range of photosynthetic organisms, either procaryotic or eucaryotic. Eucaryotic examples include *Nitella*, *Volvox*, and *Fucus*.

alkaloid

Small but complex nitrogen-containing metabolite produced by plants as a defense against herbivores. Examples include caffeine, morphine, and colchicine.

alkane (adjective aliphatic)

Compound of carbon and hydrogen that has only single covalent bonds. An example is ethane (CH₃CH₃₎.

alkene

Hydrocarbon with one or more carbon-carbon double bonds. An example is ethylene.

$$C = C$$

alkyl group

General term for a group of covalently linked carbon and hydrogen atoms such as methyl (—CH₃) or ethyl (—CH₂CH₃) groups; these groups can be formed by removing a hydrogen atom from an alkane.

allele

One of a set of alternative forms of a gene. In a diploid cell each gene will have two alleles, each occupying the same position (locus) on homologous chromosomes.

allosteric protein

Protein that changes from one conformation to another when it binds another molecule or when it is covalently modified. The change in conformation alters the activity of the protein and can form the basis of directed movement

alpha helix (α helix)

Common structural motif of proteins in which a linear sequence of amino acids folds into a right-handed helix stabilized by internal hydrogen bonding between backbone atoms.

amide

Molecule containing a carbonyl group linked to an amine. Adjacent amino acids in a protein molecule are linked by amide groups.

amino acid

Organic molecule containing both an amino group and a carboxyl group. Those that serve as the building blocks of proteins are alpha amino acids, having both the amino and carboxyl groups linked to the same carbon atom. (See Panel 2–5, pp. 56–57.)

amino acyl tRNA

Activated form of amino acid used in protein synthesis. Consists of an amino acid linked through a labile ester bond from its carboxyl group to a hydroxyl group on tRNA. (See Figure 6–12.)

amino group

Weakly basic functional group derived from ammonia (NH_3) in which one or more hydrogen atoms are replaced by another atom. In aqueous solution it can accept a proton and carry a positive charge.

amino terminus (N terminus)

The end of a polypeptide chain that carries a free $\alpha\text{-}$ amino group.

amoeba (plural amoebae)

(1) Free-living single-celled eucaryote that crawls by changing its shape. (2) More narrowly, a particular genus of protozoa that move in this way.

Amoeba proteus

Species of giant freshwater amoeba widely used in studies of cell locomotion.

amoeboid locomotion

Distinctive form of cell crawling typified by *Amoeba proteus*. Associated with the extension of pseudopodia and with cytoplasmic streaming.

AMP (adenosine 5'-monophosphate)

One of the four nucleotides in an RNA molecule. Two phosphates are added to AMP to form ATP. (*See* Figure 2–30.)

amphipathic

Having both hydrophobic and hydrophilic regions, as in a phospholipid or a detergent molecule.

anabolism

System of biosynthetic reactions in a cell by which large molecules are made from smaller ones.

anaerobio

Describes a cell, organism, or metabolic process that functions in the absence of air or, more precisely, in the absence of molecular oxygen.

anaphase

Stage of mitosis during which the two sets of chromosomes separate and move away from each other. Composed of anaphase A (chromosomes move toward the two spindle poles) and anaphase B (spindle poles move apart).

Ångstrom (Å)

Unit of length used to measure atoms and molecules. Equal to 10^{-10} meter or 0.1 nanometer (nm).

animal pole

In yolky eggs, that end free of yolk and which cleaves more rapidly than the vegetal pole.

anterior

Situated toward the head end of the body.

antibiotic

Substance such as penicillin or streptomycin that is toxic to microorganisms. Usually a product of a specific microorganism or plant.

antibody (immunoglobulin)

Protein produced by B lymphocytes in response to a foreign molecule or invading organism. Often binds to the foreign molecule or cell extremely tightly, thereby inactivating it or marking it for destruction by phagocytosis or complement-induced lysis.

anticodon

Sequence of three nucleotides in a transfer RNA molecule that is complementary to the three-nucleotide codon on a messenger RNA molecule; the anticodon is matched to